

The adult skeleton of *Spea multiplicata* and a comparison of the osteology of the pelobatid frogs (Anura, Pelobatidae)

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Among the pelobatids (Anura, Pelobatidae), the skeletal anatomy of the North American genera *Spea* and *Scaphiopus* is poorly known. Based on dry-skeletal and cleared and double-stained specimens, I describe the osteology of *Spea multiplicata* and compare it to that of all other pelobatid taxa (*Spea*, *Scaphiopus*, *Pelobates*). Several anatomical structures are shared by *Spea* and *Scaphiopus*, including the absence of a quadratojugal bone, the presence of a palatine process of the facial process of the maxilla, a long postchoanal process of the vomer, and a completely cartilaginous sternum. *Spea* is characterized by a poorly developed maxillary process of the nasal, the lack of a well-developed posteromedial process of the parasphenoid, and possibly a well-developed pars ascendens plectri of the auditory apparatus. Most other diagnostic features of *Spea* relate to the limited cranial ossification of this genus relative to other members of the family.

INTRODUCTION

Among "basal" frogs, the largest and arguably the most poorly known group is the Pelobatoidea. These frogs comprise about 95 extant species (FROST, 1985) in three families (Pelobatidae, Megophryidae and Pelodytidae), and are distributed throughout the Holarctic Region extending into the Old World tropics (DUELLMAN & TRUEB, 1994). Among the Pelobatidae are frogs in the genera *Pelobates*, *Scaphiopus* and *Spea*. Although the skeletal anatomy of frogs in the genus *Pelobates* has been considered by several authors (e.g., ANDERSEN, 1978; ROČEK, 1981; RODRÍGUEZ TALAVIRA, 1990), the adult osteology of the North American genera *Spea* and *Scaphiopus* remain poorly understood.

Of the few authors who have considered the skeleton of the North American pelobatids, JURGINS (1971) included *Spea intermontana* in his description of the nasal cartilages of anurans, RAMASWAMI (1939) described the cranial osteology of *Scaphiopus holbrookii*, and FABREZI (1992) described the carpus of *Scaphiopus couchii*. The only thorough description of the anatomy of these frogs is that by WILNS (1989) on the osteological development of *Spea bombifrons*. It is in part because of the lack of detailed morphological descriptions of *Spea*

and *Scaphiopus* that the phylogenetic relationships within the family Pelobatidae are unresolved (FORD & CANNATELLA, 1993). Therefore, I provide a detailed description of the adult skeleton of *Spea multiplicata*, a species for which the anatomy is relatively unknown, and compare its skeleton to that of other frogs in the family Pelobatidae, with the hope of attaining information that may be phylogenetically useful.

MATERIALS AND METHODS

Osteological descriptions of *Spea multiplicata* were made from male and female dried skeletons and cleared and double-stained specimens. Dry-skeletal and cleared and double-stained specimens of *Spea bombifrons*, *S. hammondu*, *S. intermontana*, *Scaphiopus couchii*, *S. holbrookii*, *S. hurterii*, *Pelobates cultripes*, *P. fuscus*, *P. syriacus* and *P. varaldii* also were examined (app. 1). Osteological terminology is that of DE SÁ & TRUEB (1991), TRUEB (1993), DUELLMAN & TRUEB (1994) and FABREZI & ALBERCH (1996, for manus and pes). Descriptions and illustrations were made with the aid of a stereo microscope equipped with a camera lucida.

RESULTS

CRANIUM

The cranium is square and well ossified, but lacks dermal ornamentation (fig. 1). Both the neopalatine and quadratojugal are absent in this species. The frontoparietal fontanelle is exposed as a moderate-sized fenestra, and the maxillae and premaxillae bear teeth.

Nasal cartilages

The septum nasi is extensively ossified, synostotically fused to the sphenethmoid, and extends forward anterior to the nasal roofing bones. The tectum nasi also is ossified and is invested by the medial margins of the nasals. The oblique cartilages, which form the anterodorsal roof of the nasal capsule, are confluent anteromedially with the septum and tectum nasi and posterolaterally with the commissura lateralis (fig. 2). A minute and blunt anterior maxillary process projects forward from the anteroventral border of the planum antorbitale toward the posterior half of the facial process of the maxilla. The posterior maxillary process projects posteriorly from the posteroventral margin of the planum antorbitale, and is fused synchondrotically to the pterygoid process of the palatoquadrate cartilage. The anterolateral margin of the oblique cartilage unites with the robust crista subnasalis, which extends ventrally to abut the anterior margin of the facial process of the maxilla. Posteriorly, the crista subnasalis fuses with the solum nasi, the horizontal sheet of cartilage extending medially from the septum nasi that forms the floor of the nasal capsule. A small, bifurcate process extends posteriorly from the solum nasi to articulate with the sphenethmoid and the dorsal surface of the vomer. The cup-shaped alary cartilage lies above the anterior margin of the solum nasi, providing support for the anterior margin of the nares. The alary cartilage is united synchon-

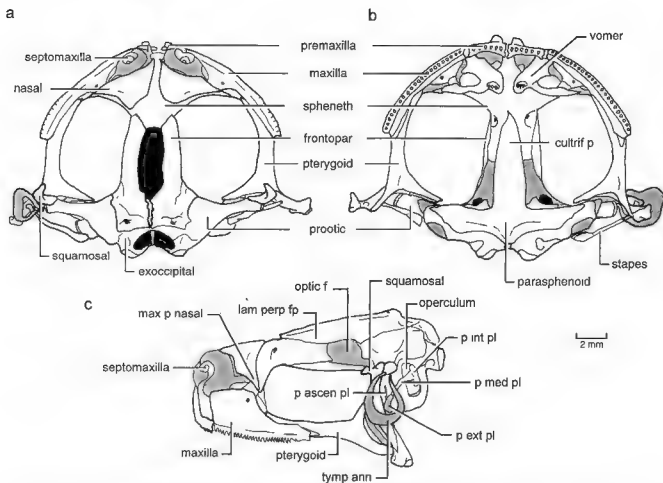


Fig 1 Cranium of *Spea multiplicata* (KU 86662) in (a) dorsal, (b) ventral, and (c) lateral view. Gray denotes cartilage, black denotes foramina. Abbreviations: cultrif p, cultriform process of parasphenoid; f, foramen; frontopar, frontoparietal; lam perp fp, lamina perpendicularis of frontoparietal; max p nasal, maxillary process of nasal; p ascen pl, pars ascendens plectri; p ext pl, pars externa plectri; p int pl, pars interna plectri; p med pl, pars media plectri; spheneth, sphenethmoid; tymp ann, tympanic annulus.

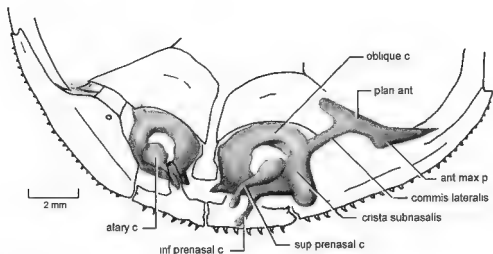


Fig. 2. Nasal cartilages of *Spea multiplicata* (KU 86664) in oblique anterior view. Gray denotes cartilage, white denotes bone. Abbreviations. ant max p, anterior maxillary process; c, cartilage, commis, commissura, inf, inferior; plan ant, planum antorbitale; sup, superior

drodically with the superior prenasal cartilage, which extends ventromedially to the alary process of the premaxilla. The inferior prenasal cartilage extends anteroventrally from the solum to the premaxilla.

Septomaxillae

Each of these small bones lies medial to the fusion of the oblique cartilages and the crista subnasalis, and posterior to the alary cartilage (fig. 2). Although complex in shape, only the medial and lateral rami are exposed in dorsal view (appearing to be U-shaped).

Sphenethmoids

These extensively ossified elements are fused dorso- and ventromedially to form a single bone, exposed dorsally in a diamond-shaped area between the frontoparietals and the nasals (fig. 1a). Anteriorly, the ossified septum nasi is synostotically fused to the sphenethmoid, forms the shared medial wall of the nasal capsules, and extends forward beyond the length of the nasal roofing bones. Ventrally, the sphenethmoid floors the nasal capsules, extending anteriorly to the level of the pars palatina of the premaxilla (fig. 1b). The sphenethmoid extends laterally for most of the planum antorbitale to articulate with the pars facialis of the maxilla. Ventromedially, the orbitonasal foramen opens posteriorly at the level of the anterior margin of the cultriform process. Dorsomedial ossification includes the anterior margin of the frontoparietal fontanelle; posteroventral and lateral ossification continues to the level of the anterior margin of the optic foramen, thereby forming the anterolateral wall of the neurocranium.

Prootics and exoccipitals

The prootics and exoccipitals are synostotically united with one another. The prootics form the anterior and ventrolateral parts of the otic capsule, and are invested dorsomedially by the frontoparietals (fig. 1a). The posterolateral margin of the frontoparietal extends to the eminentia epiotica. Each prootic forms the posterior margin of the optic foramen; anterior ossification extends only to the posterior three fourths of the prootic foramen. Laterally, the prootic narrows to form an extensively ossified crista parotica, with only the distal tip being cartilaginous. The lateralmost tip of the prootic, ventral to the crista parotica, is mineralized and articulates with the basal process (sensu REISS, 1997) of the pterygoid.

The exoccipitals form the posteromedial part of the otic capsule, as well as the margin of the foramen magnum and the occipital condyles. The hyal of the hyoid attaches to the posterolateral margin of the exoccipital, and possibly to the posterior margin of the basal process, via a small ligament (or other unstained connective tissue). The margin of the foramen magnum is incompletely ossified dorsomedially and dorsoventrally (fig. 1b). The occipital condyles, lateral to the foramen magnum, are well developed. Internal and slightly lateral to the occipital condyles are the jugular foramina.

Plectral apparatus

The plectral apparatus is ventral to the crista parotica, oriented horizontally (fig. 1b-c). The fully ossified pars interna plectri is expanded but separate from the fenestra ovalis and operculum. The operculum is robust and completely ossified, except for the posterolateral margin. The pars media plectri is columnar, slightly sigmoidal, and expanded medially to articulate with the pars interna plectri. Distally, the pars externa plectri forms a flat cartilaginous plate that fills about one-third of the tympanic annulus. A well-developed pars ascendens plectri extends from the medial portion of the pars externa plectri to the crista parotica. The tympanic annulus attaches dorsally to the cartilaginous tip of the crista parotica, and except for a slight separation at this articulation, forms a complete ring.

Nasals

The rhomboidal, paired nasals overlie the nasal capsule (fig. 1a). Medially, they overlap the septum nasi of the sphenethmoid, although this element is clearly visible between them. Posteriorly, the nasals overlap the planum antorbitale, but do not articulate with the frontoparietals. Laterally, the poorly-developed maxillary process of each nasal narrows to extend to the level of the pars facialis of the maxilla, but does not articulate with it.

Frontoparietals

These paired, dorsal elements form the lateral and posterior margins of the frontoparietal fenestra (fig. 1a). Anteriorly, they invest the sphenethmoid to the level of the tectum anterior; anterolaterally, each narrows away from the anterior margin of the fenestra and lacks a supraorbital flange. Laterally, each forms the lamina perpendicularis, which extends

ventrally about one third of the height of the braincase and posteriorly to the anterior margin of the optic foramen (fig. 1c). Posterodorsally, these elements overlap the prootic to the eminentia epiotica. A narrow ridge, the occipital crest, forms anterior to the eminentia epiotica. Anterior to this crest, the occipital foramen opens posteriorly. Although completely covered, the occipital canal is visible through the bone, traversing obliquely from the lateral margin of the frontoparietal to open at the level of the posterior margin of the frontoparietal fenestra. In some specimens, a smaller foramen opens dorsally at the midpoint of the occipital canal.

Parasphenoid

The parasphenoid is broad, smooth, and lacks bony ornamentation. The anterior half of the broad cultriform process overlaps the sphenethmoid, and narrows to a point just posterior to the level of the planum antorbitale (fig. 1b). The parasphenoid alae are broad, anterolaterally oriented, and ventrally invest the otic capsule. A distinct posteromedial process is absent; however, the posterior margins of the alae converge to form the posteromedial margin. This part underlies the ventral cartilaginous margin of the foramen magnum (between the exoccipitals).

Vomers

The vomers are large, bear about five teeth each, and contribute to the floor of the nasal capsules (fig. 1b). The anterior process is rectangular and extends obliquely from its anterior margin just posterior to the maxilla-premaxilla articulation toward the midline of the body. At the level of the dentigerous process, a small prechoanal process extends laterally. Medial to this process is a small foramen for the palatine ramus of the facial nerve. The dentigerous process is rounded, and narrowly separated from its counterpart. The postchoanal process is long and slender, and invests the planum antorbitale. This process extends beyond the planum antorbitale to articulate at its most dorsolateral end with the anterior ramus of the pterygoid via the posterior maxillary process of the planum antorbitale and may articulate weakly with the pars facialis of the maxilla.

Premaxillae

The premaxillae are narrowly separated from one another; each has a well-developed alary process that is inclined anteriorly, curved slightly laterally, and ends dorsally in a bifurcated, rounded tip. The pars dentalis curves dorsolaterally; its anteroventral surface appears wavy because of the presence of approximately 12 teeth (fig. 1b). The palatine process of the pars palatina is a short, flat plate that forms a right triangle. A small posterolateral process of the pars palatina also is present.

Maxillae

Each maxilla possesses approximately 36 teeth and lacks pre- and postorbital processes. The pars facialis of each is well developed and reaches its maximum height at the level of

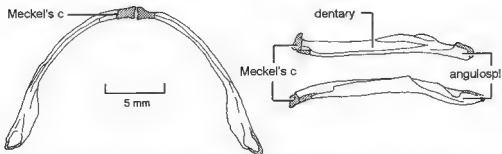


Fig. 3. Mandible of *Spea multiplicata* (KU 86664) in dorsal (left), lateral (right, top), and lingual (right, bottom) view. Gray denotes cartilage. Abbreviations: angulospl, angulosplenic; c, cartilage.

the planum antorbitale (fig. 1c). The anterior tip of the pars facialis articulates with the lateral margin of the premaxilla and the medial margin articulates with the planum antorbitale of the sphenethmoid. A small foramen, possibly a foramen for a ramus of the maxillaris superior vessels, traverses vertically through the pars facialis.

Mandible

The angulosplenic, dentary, and mentomeckelian bones comprise the mandible (fig. 3). The mentomeckelian bones form the anterior margin of the mandibles; they are small and relatively well ossified, and are fused to one another medially. The thin dentary articulates with the posterior portion of the mentomeckelian, and extends posteriorly for more than half the length of the mandible, investing the lateral margin of Meckel's cartilage. The angulosplenic forms the posterior portion of the mandible and serves as the attachment point for the mandible to the cranium. The angulosplenic extends anteriorly to invest most of the lingual margin of Meckel's cartilage. Posteromedially, the angulosplenic possesses a well-developed coronoid process.

Squamosals

The zygomatic ramus of the squamosal is short and projects anteriorly (fig. 1c). The otic ramus of the squamosal invests the anterolateral tip of the crista parotica. The ventral ramus extends posteroventrally at a 45° angle relative to the horizontal axis of the skull and invests the ossified portion of the palatoquadrate cartilage. A thin, sheetlike process extends anteromedially from the ventral ramus, ventral to the zygomatic ramus, and invests the palatoquadrate cartilage.

Pterygoids

The triradiate pterygoids are well developed, with robust anterior and medial rami (fig. 1a-b). The anterior ramus projects anterodorsally, invests the pterygoid process of the palatoquadrate, and articulates with the pars palatina of the maxilla. The anterior ramus

synchondrotically fuses to the lateral margin of the postchoanal process of the vomers. The posterior ramus invests the ventrolateral surface of the pars articularis of the palatoquadrate. The medial ramus invests the pterygoid process of the palatoquadrate and articulates with the basal process.

Palatoquadrates

The pars articularis of the palatoquadrate (quadrate process) is ossified to the level of midheight of the ventral process of the squamosal. The basal process extends medially to articulate with the prootic, and is invested by the medial ramus of the pterygoid (fig. 1c).

HYOID APPARATUS

Hyoid apparatus

There is little sexual dimorphism in the hyoid apparatus. The hyoid plate shows no mineralization and is narrow, the length along the longitudinal axis (midlength) is about two-thirds the length along the transverse axis (fig. 4). The hyoglossal sinus is U-shaped. Separate anterolateral processes are not present; they are fused to the hyoid plate in development, creating oval lateral foramina (WIENS, 1989), which are larger in males. As in other pelobatoids (CANNATELLA, 1985), the hyals are disassociated from the hyoid plate, with each ventrally investing the lateral margin of the hyoid plate, posterior to the lateral foramen, narrowing posterolaterally, and extending forward to articulate with the exoccipital (or basal process of the palatoquadrate; see *Exoccipitals* above).

The slender posterolateral processes project from the posterior margin of the hyoid plate at approximately a 45° angle to the transverse axis of the hyoid plate. These processes are about equal in length to the midlength of the hyoid plate. The ossified posteromedial processes project posterolaterally from the posteromedial margin of the hyoid plate at approximately a 60° angle to the transverse axis of the hyoid plate. In males, the shaft of each posteromedial process is one-third the width of the proximal and distal heads; in females, the shaft is half the width of either head.

Laryngeal cartilages

There is sexual dimorphism in both the size and shape of the laryngeal cartilages. In males, the laryngeal apparatus nearly fills the entire space between the posteromedial processes; in females, only half of this space is filled. In ventral view, the paired arytenoid cartilages, which are much larger in males, lie within the cricoid ring. As each of these cartilages extends dorsomedially, it becomes more narrow and less concave, and appears to form discrete dorsal and ventral parts (fig. 4). In males, the dorsal portion extends almost the full length of the ventral portion. In females, the dorsal portion is only half the length of the ventral part, and the anterodorsal margin is acuminate. The elongate, paired bronchial processes project ventrolaterally from the cricoid ring at the level of the distal heads of the posteromedial processes. The distal portion of each bronchial process terminates in a head with three

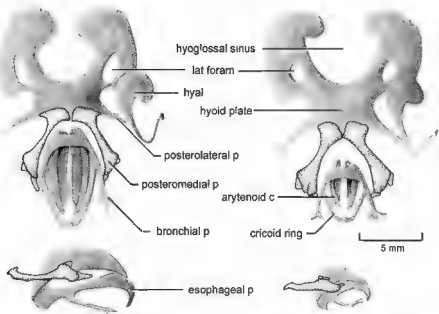


Fig 4 – Ventral view of hyoid apparatus (top) and lateral view of cricoid ring (bottom) of male (left, KU 86664) and female (right; KU 86662) *Spea multiplicata*. Stippled pattern denotes bone, gray denotes cartilage. Abbreviations: c, cartilage, lat foram, lateral foramen; p, process.

fingerlike projections. In males, the bronchial processes extend to the level of the posterior margin of the arytenoid cartilages; in females, these processes extend to the level of the posterior margin of the cricoid ring. Slightly posterior to the origin of the bronchial processes, shelf-like expansions extend medially from the cricoid ring. In males, a small square esophageal process extends ventrally from the posterior margin of the cricoid ring; in females, this process is less distinct.

AXIAL SKELETON

The vertebral column is composed of eight notochordal presacral vertebrae, the sacrum and the urostyle (fig. 5a). The vertebrae are slightly imbricate, and ossified intervertebral bodies are present between the centra. Each neural arch bears a low neural ridge with two small, posterior projecting spinous processes; the articular facets of the pre- and postzygapophyses are simple. The relative lengths of transverse processes and sacral diapophyses are as follows: III > sacrum = IV > II > V ≈ VI ≈ VII ≈ VIII. Transverse processes of presacrals III-V are almost perpendicular to the notochordal axis, whereas those of presacrals II, VI, VII and VIII are directed anteriorly. Small, posteriorly directed uncinuate processes are present on the transverse processes of vertebrae II-IV.

The cervical cotyles of the atlas are Type II (LYNCH, 1973) and are nearly contiguous. The urostyle is rounded in cross section, fuses with the sacrum, and bears a dorsal ridge.

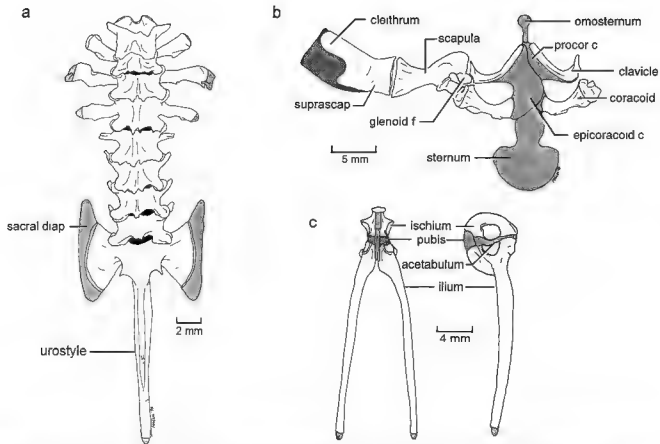


Fig. 5 (a) Dorsal view of axial skeleton of *Spea multiplicata* (KU 86664). (b) Ventral view of pectoral girdle (KU 86662), with the scapula and suprascapula deflected ventrally. (c) Ventral (left) and lateral view of pelvic girdle (KU 86664) Gray denotes cartilage. Abbreviations. c, cartilage, f, fossa; procor, procoracoid; sacral diap, sacral diapophysis, suprascap, suprascapula.

throughout its anterior two thirds. The sacrum consists of vertebrae IX and X, and the slightly expanded sacral diapophyses (expanded transverse processes of vertebrae IX, WIENS, 1989) are oriented perpendicular to the midline of the body. A bony webbing, which has been mistaken for postsacral transverse processes (discussed by WIENS, 1989), is present on the posterior margin of the sacrum, between vertebrae IX and X.

APPENDICULAR SKELETON

Pectoral girdle

The sternum is a spade-shaped plate of cartilage that floats between the epicoracoid cartilages, typical of the arciferal arrangement of the girdle (fig 5b). A completely cartilaginous, knob-shaped omosternum articulates with the epicoracoid bridge of the epicoracoid cartilages. The anterior margins of the paired procoracoid cartilages are completely invested by the clavicles and are synchondrotically contiguous posteromedially with the epicoracoid cartilages. The pectoral fenestrae are large and tear-shaped, each is bordered anteriorly by the procoracoid cartilage, medially by the epicoracoid cartilage, posteriorly by the coracoid, and laterally by the glenoid fossa.

The relatively long clavicles (one-third longer than the coracoids) are posteriorly concave; the glenoidal end of each is flared anteriorly, forming a wedge-shaped process that abuts the pars acromialis of the scapula. The clavicles do not reach the midline and are separated medially by the epicoracoid bridge. The long axes of the coracoids are slightly arcuate; each of these robust bones is narrowly separated anterolaterally from the clavicle and articulates with the pars glenoidalis of the scapula. The sternal end of each coracoid is moderately broad (twice the width of the shaft), but narrower than the glenoidal end (approximately 80% of width of glenoidal end). The scapular end of the coracoid is also broad (almost three times the width of the shaft) and its distal concavity articulates with the pars acromialis, forming the posterior surface of the relatively deep glenoid fossa.

The scapula is about three times the length of the glenoid fossa, with its greatest width being half of its total length. The pars glenoidalis is a thin, concave plate, and the pars acromialis is a robust, rounded process; both form the remaining portion of the glenoid fossa. The shaft of the scapula is short and constricted (width about one-fourth total length of scapula). The distal head of the scapula is expanded to articulate with the cleithrum; its width is twice the width of the shaft and half the total length of the scapula. The cleithrum invests most of the anterior two-thirds of the suprascapular cartilage. It is narrow anterodistally and broadens at the scapular end to form the shape of a cleaver. The suprascapular cartilage extends posteriorly as a broad, flat blade.

Forelimb

The humerus has a large, flangelike crista ventralis, a slightly smaller, well-developed crista medialis, and a low crista lateralis. The glenoid head of the humerus (caput humeri) is cartilaginous, whereas the distal head (eminentia capitata) is completely ossified. The flattened radioulna is about two-thirds the length of the humerus and its distal head is wider than

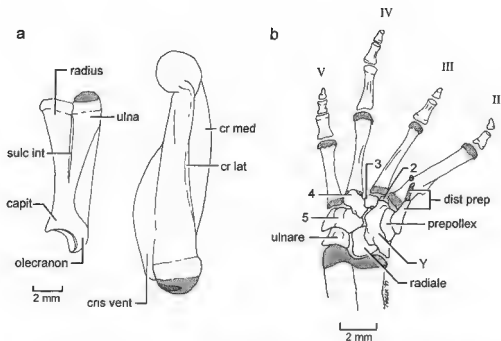


Fig. 6 - Right forelimb of *Spea multiplicata* (KU 86664); top of figure is anterior. (a) Dorsal view of radioulna (left) and lateral view of humerus. (b) Ventral view of hand. Gray denotes cartilage. Abbreviations. capit, capitulum, cr lat, crista lateralis; cr med, crista medialis, crs vent, crista ventralis; dist prep, distal prepollex; sulc int, sulcus intermedius, u, ulnare, Y, element Y.

its proximal head (fig. 6a). A distinct groove, the sulcus intermedius, distinguishes the radius and ulna, although they are fused to one another medially. A small flange is present along the proximolateral edge of the ulna.

The manus resembles that of *Scaphiopus couchii* (morphology A) as described by FABREZI (1992). Proximally, there is a small ulnare, and a slightly larger radiale; distally, there is a large irregular-shaped element Y and a smaller carpal 5 (fig. 6b). Carpals 2, 3 and 4 lie proximal to metacarpals II, III and IV, respectively. Carpals 3 and 4 are partially fused to one another, and lie on the ventral surface of the manus; carpal 2 is smaller, and lies dorsal to element Y. All carpal elements are well ossified. A moderate-sized, ossified prepollex lies distomedial to element Y. One completely ossified distal prepollical element and at least one cartilaginous distal prepollex also are present. Relative lengths of the digits are $IV > II > III \approx V$. The phalangeal formula is 2-2-3-3. There is apparent sexual dimorphism in the size and shape of digit II, in male specimens, the metacarpal and phalanges are thickened, with a small protuberance on the medial border of the metacarpal.

Pelvic girdle

In dorsal view, the internal margins of the ilia form a narrow U-shape (fig. 5c). The ilial shafts are simple, with no obvious crests, but have a small dorsal prominence. The preacetabulum is moderate and the preacetabular angle (i.e., the angle between the ilial shaft and the preacetabular margin) is slightly obtuse. The ilia are separated from one another medially and from the ischia posteriorly by cartilage. The ischia are approximately D-shaped, and are fused to one another to form the posterior margin of the acetabulum. The completely cartilaginous pubis forms the ventral border of the acetabulum.

Hind limb

The femur is long and thin (length about 12 times width); both the distal and acetabular heads are cartilaginous. The femur possesses a small ridge on the lateral margin. The tibiofibula is about three-fourths the length of the femur, and its distal and proximal heads are of similar size. Although the tibia and fibula are fused, a distinct groove separates them. The tibiale and fibulare are short and robust (length less than half that of the tibiofibula), and are fused to one another at their proximal and distal heads (fig. 7a).

The pes has a single ossified tarsal element proximal to digit II, and a large element Y (FABREZI, 1993) proximal to metatarsal I (fig. 7b). An ossified prehallux and a large spadelike distal prehallal element are present medial to element Y. Relative lengths of the digits are $IV > V > III > II > I$. The phalangeal formula is 2-2-3-3-3.

DISCUSSION

Although the anatomy of frogs in the genus *Pelobates* is relatively well known, the phylogenetic relationships within the family Pelobatidae are unresolved (FORD & CANNATELLA, 1993), in part because of a lack of detailed morphological descriptions of the other members of the family, *Spea* and *Scaphiopus*. The description provided herein should facilitate a more detailed comparison among pelobatid taxa. What follows is both a summary of the most recent works on pelobatid osteology as well as my own observations. The preliminary comparisons of *Spea multiplicata* to all other pelobatid taxa presented here were incorporated as part of a phylogenetic analysis of the pelobatids (MAGLIA, 1998).

Most recent authors (e.g., FORD & CANNATELLA, 1993, DUELLMAN & TRUEB, 1994) agree that pelobatids (*Pelobates*, *Scaphiopus* and *Spea*) form a monophyletic assemblage. However, although there are several diagnostic characters for these frogs (including broad sacral diapophyses and sculpturing of dermal cranial bones, ROČEK, 1981), few osteological features have been proposed to be shared derived characters uniting *Pelobates*, *Scaphiopus* and *Spea*. CANNATELLA (1985) proposed that the presence of cranial exostosis and a long zygomatic ramus of the squamosal were synapomorphies for the pelobatids, however, both of these features are absent in the genus *Spea*. He also cited the presence of a supraorbital flange of the frontoparietal in all pelobatids, however, I have not seen evidence of this structure in any

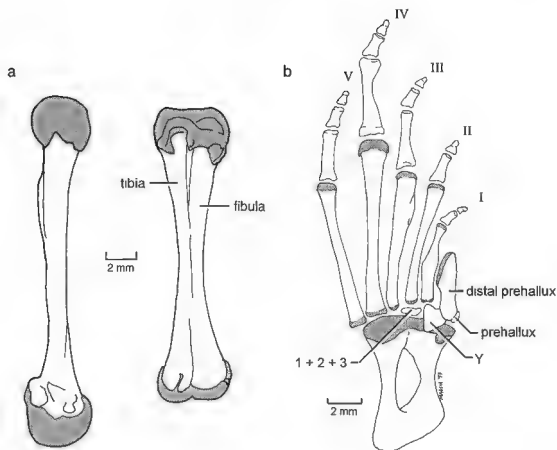


Fig. 7. Right hind limb of *Spea multiplicata* (KU 86664) (a) Lateral view of femur (left) and ventral view of tibiofibula (b) Ventral view of right foot. Gray denotes cartilage. Abbreviation Y, element Y.

Spea. The other osteological characters uniting the pelobatids in CANNATELLA'S (1985) analysis, the complete ossification of septum nasi and the fused articulation of the urostyle and sacrum, are found in several non-pelobatid taxa.

In comparing the osteology of *Spea multiplicata* with that for all other pelobatid taxa, I found several features shared by the pelobatids. All of these taxa possess an occipital canal that is roofed completely by bone. This feature is not present in non-pelobatid pelobatoids (e.g. *Megophrys*, *Pelodytes*), however, it is present in other taxa (e.g. some neobatrachians LYNCH, 1969, MENDILSON et al., in press). The presence of bony webbing on the posterior margin of the sacral diapophyses is shared among all pelobatids. This has been identified by some authors (e.g. LYNCH, 1973, DULLIMAN & TRUIB, 1994) as post-sacral transverse processes, but was shown to originate in development from the sacral diapophyses (WIENS,

1989). Other morphologies shared by all pelobatids are the presence of relatively elongate, convex clavicles and well-developed facial and preorbital processes of the maxilla.

The North American pelobatids *Spea* and *Scaphiopus* have several morphological features that are unique to them, including the lack of a quadratojugal bone and the presence of a palatine process of the facial process of the maxilla (CANNATELLA, 1985). These taxa also possess a postchoanal process of the vomer that subtends the planum antorbitale (discussed in CANNATELLA, 1985) and a completely cartilaginous sternum. ROČEK (1981: 151) provided a detailed comparison of the cranial differences between *Pelobates* and the North American pelobatids, and included a discussion of several features common to *Scaphiopus* and *Spea* (e.g., well-developed stapes, ossified operculum).

Several morphologies are unique to the genus *Spea*. For example, *Spea* lacks the exostosis of the dermal cranial and suspensorium elements found in all other pelobatids. Also, the otic ramus of the squamosal barely overlaps the crista parotica, whereas it forms an otic plate investing nearly half the otic capsule in other pelobatids. Also in *Spea*, the frontoparietals do not come into contact with the nasals; they lack supraorbital flanges, and they are in contact posteromedially only, exposing the frontoparietal fontanelle. These features most likely relate to the degree of ossification of the cranium of *Spea*: these frogs are much less ossified than other pelobatids. If *Scaphiopus* and *Spea* share a most common ancestor, which seems to be of little doubt (FORD & CANNATELLA, 1993; DUELLMAN & TRUEB, 1994), and if the clade [*Spea* + *Scaphiopus*] is the sister group to *Pelobates* (also well supported; CANNATELLA, 1985), then the limited ossification and small body size of *Spea* may be a reversal of the hyperossification present in *Pelobates* and *Scaphiopus*. However, it is just as likely that the common ancestor shared by the Pelobatidae resembled *Spea* in amount of ossification, and that the hyperossification present in *Pelobates* and *Scaphiopus* evolved separately in these taxa.

Morphologies are thought to be highly conserved among species of *Spea*, and primarily one morphological feature, the frontoparietal boss, has been the subject of much discussion (WIENS & TITUS, 1991). Therefore, the only major works attempting to analyze the relationships within the genus *Spea* have relied on biochemical data (e.g., SAGE et al., 1982; WIENS & TITUS, 1991). However, comparing *S. multiplicata* to other members of the genus, I found several features that vary to some degree among these frogs. For example, the maxillary process of the nasal is poorly developed in *S. multiplicata* and *S. bombifrons*, but is more extensive in the other taxa. Similarly, *S. multiplicata* and *S. bombifrons* lack a well-developed posteromedial process of the parasphenoid, whereas the other taxa possess this feature.

A small but striking anatomical feature present in *Spea multiplicata* is a well-developed pars ascendens plectri of the auditory apparatus. Because this feature can only be observed on cleared and double-stained specimens with well-developed plectral apparatuses, I was able only to compare it among a few taxa in this sample (*S. bombifrons*, *Scaphiopus couchii* and *Pelobates varuldi*). Of these, the pars ascendens plectri was only present in *S. bombifrons* (although not described by WIENS, 1989). This structure may be unique to *Spea* or may vary among pelobatids. It is hoped that further comparisons of this feature and others discussed here will help in resolving the relationships among the pelobatids.

RESUMEN

Entre los pelobátidos (Anura, Pelobatidae), la morfología esquelética de los géneros norteamericanos *Spea* y *Scaphiopus* es pobremente conocida. La osteología de *Spea multiplicata* se describe en base a esqueletos secos y a especímenes diafanizados y doblemente teñidos, y se la compara con todos los otros taxones de pelobátidos (*Spea*, *Scaphiopus*, *Pelobates*). *Spea* y *Scaphiopus* comparten varias morfologías, incluyendo la ausencia de cuadradojugal, la presencia de un proceso palatino del proceso facial de la maxila, proceso postcoanal del vomer largo, y esternon completamente cartilaginoso. *Spea* se caracteriza por un proceso maxilar del nasal pobremente desarrollado, falta de un proceso postero-medial de parasfenoides bien desarrollado y posiblemente una pars ascendens plectri del aparato auditivo bien desarrollada. La mayoría del resto de los caracteres diagnósticos de *Spea* están relacionados a la limitada osificación craneal de este género en relación a otros miembros de la familia.

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LITERATURE CITED

- ANDERSEN, M. L., 1978. *The comparative myology and osteology of the carpus and tarsus of selected anurans*. PhD Thesis, Lawrence, The University of Kansas. 1-302.
- CANNATELLA, D. C., 1985. *A phylogeny of primitive frogs (Archaeobatrachians)*. PhD Thesis, Lawrence, The University of Kansas. 1-404.
- DUELLMAN, W. E. & TRUEB, L., 1994. *Biology of amphibians*. Second edition. Baltimore, Johns Hopkins University Press. i-xix + 1-670.
- FABREZI, M., 1992. - El carpo de los anuros. *Alytes*, **10**: 1-29.
- 1993. - The anuran tarsus. *Alytes*, **11**: 47-63.
- FABREZI, M. & ALBERCH, P., 1996. The carpal elements of anurans. *Herpetologica*, **52**: 188-204.
- FORD, L. S. & CANNATELLA, D. C., 1993. The major clades of frogs. *Herp Mon*, **7**: 94-117.
- FROST, D. R., (ed.), 1985. *Amphibian species of the world*. Lawrence, Allen Press & Assoc. Syst. Coll. [i-iv] + i-v + 1-732.
- JURGENS, J. D., 1971. The morphology of the nasal region of the Amphibia and its bearing on the phylogeny of the group. *Ann. Univ. Stellenbosch*, **46**: 1-146.
- LYNCH, J. D., 1969. *Evolutionary relationships and osteology of the frog family Leptodactylidae*. PhD Thesis, Lawrence, The University of Kansas. 1-800.
- 1973. The transition from archaic to advanced frogs. In: J. L. VIAL (ed.), *Evolutionary biology of the anurans: contemporary research on major problems*. Columbia, Univ. of Missouri Press. 133-182.
- MAGLIA, A. M., 1998. Phylogenetic relationships of the pelobatid frogs (Anura, Pelobatoidea): skeletal evidence. *Sci. Pap. nat. Hist. Mus. Univ. Kansas*, **10**: 1-19.

- MENDELSON, J. R., III, DA SILVA, H. R. & MAGLIA, A. M., in press – Phylogenetic relationships among genera of marsupial frogs (Anura Hylidae: Hemiphraclininae), based on evidence from morphology: reassessment of character and life history evolution *Zool J. Linn. Soc.*, in press.
- RAMASWAMI, L. S., 1939. The cranial morphology of some examples of Pelobatidae (Anura) *Anat. Anz.*, **81**: 65-96.
- REISS, J. O., 1997. Early development of chondrocranium in the tailed frog *Ascaphus trueti* (Amphibia Anura): implications for anuran palatoquadrate homologies. *J. Morph.*, **231**: 63-100.
- ROČEK, Z., 1981. – Cranial anatomy of frogs in the family Pelobatidae Stannius, 1856, with outlines of their phylogeny and systematics. *Acta Univ. Carol. Biol.*, **1980**: 1-164.
- RODRÍGUEZ TALAVERA, M.-R., 1990. – *Evolución de peloditidos morfología y desarrollo del sistema esquelético*. PhD Thesis, Madrid, Universidad Complutense de Madrid 1-282.
- SÁ, R. O., DE & TRUEB, L., 1991. – Osteology, skeletal development, and chondrocranial structure of *Hamptophryne boliviana* (Anura, Microhylidae) *J. Morph.*, **209**: 311-330.
- SAGE, R. D., PRAGER, E. M. & WAKE, D. B., 1982. A Cretaceous divergence time between pelobatid frogs (*Pelobates* and *Scaphiopus*). immunological studies of albumin serum *J. Zool.*, London, **198**: 481-494.
- TRUEB, L., 1993. Patterns of cranial diversity among the Lissamphibia. In J. HANKEN & B. K. HALL (ed.), *The skull, 2, Patterns of structural and systematic diversity*, Chicago, The University of Chicago Press: 255-341.
- WIENS, J. J., 1989. – Ontogeny of the skeleton of *Spea bombifrons* (Anura: Pelobatidae) *J. Morph.*, **202**: 29-51.
- WIENS, J. J. & TITUS, T. A., 1991. – A phylogenetic analysis of *Spea* (Anura: Pelobatidae) *Herpetologica*, **47**: 21-28.

APPENDIX I SPECIMENS EXAMINED

INSTITUTIONS

AMNH: American Museum of Natural History, New York, USA.

KU: The University of Kansas, Lawrence, USA.

MCZ: Harvard University Museum of Comparative Zoology, Cambridge, USA.

MNCN: Museo Nacional de Ciencias Naturales, Madrid, Spain.

SPECIMENS EXAMINED

Pelobates cultripes: KU 148619, MNCN 20041

Pelobates fuscus: KU 68819, 129240

Pelobates syriacus: KU 146856.

Pelobates varaldi: AMNH 62935, MCZ 31970

Scaphiopus couchii: KU 20444, 73384, 209575

Scaphiopus holbrookii: KU 20439, 145413.

Scaphiopus hurteri: KU 20472, 60173, 90096.

Spea bombifrons: KU 5405, 73382

Spea hammondi: KU 176016.

Spea intermontana: KU 79436, 204563

Spea multiplicata: KU 27622, 39776A, B, 49468, 84888, 86662, 86664, 97355, 106225, 117347

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